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ON THE GENERIC LIMITS IN THE FAMILY PILIDAE (PROSOBRANCHIA: MOLLUSCA)¹

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I

Members of the molluscan family Pilidae have been known to science since pre-Linnaean times. Although the family has been defined, the generic limits — and particularly generic relationships — require further clarification. Morphologic investigations have been conducted on representatives of individual species, but only rarely have these studies been of a comparative nature. An attempt has been made in the present paper to review and collate the available information upon which generic limits may be established. Studies on the comparative morphology of the kidney and the penial complex are also presented.

In the following discussion the family Pilidae will be considered to consist of seven genera. Included in the genera *Pila*, *Lanistes*, *Afropomus*, and *Saulca* are the Old World species; members of *Pomacea*, *Marisa*, and *Asolene* constitute the New World species. These genera have been erected primarily upon conchological characteristics based on such criteria as color, size and shape of the shell, types of sculpturing (if present), and the presence or absence of an umbilicus.

II

Attempts have been made by others to divide the family into two major groups, the Old and New World forms, on the presence or absence of a calcareous operculum. Newer knowledge

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has shown that this criterion is unsound, since only *Pila* has a calcareous operculum. However, the phylogenetic significance of the operculum even in *Pila* is limited since calcification is a secondary process which occurs after the snail hatches (Ranjah, 1942).

The longisiphonate or brevisiphonate nature of the respiratory siphon has also been used as a criterion for the separation of Old and New World species, and appears to have some validity. *Pila* and *Lanistes* are brevisiphonate, and the present study indicates that the siphon of *Afropomus* is similar. *Saulea* can only tentatively be accepted as a valid genus since no description of its anatomy exists. The New World genera, *Pomacca* and *Marisa*, are longisiphonate; however, *Asolcne* has been reported (Scott, 1943) to have an aberrant siphon (brevisiphonate ?), and may be closely related to the Old World genera. It has been suggested that the morphology of the siphon is not of phylogenetic significance, but reflects an adaptation to ecological conditions (Prashad, 1925).

The radulae of the Pilidae are all taenioglossate and have the formula 2:1:1:1:2. Intra-specific variations, however, reduce the value of radular morphology at levels below the family. The genus *Turbinicola* was erected on the basis of radular morphology (Annandale and Prashad, 1921; Prashad, 1931); however, Pilsbry and Bequaert (1927) consider this group to be no more than a subgenus of *Pila*.

The eggs of the various species provide several promising and characteristic differences which may aid in arriving at taxonomic limits of the genera. Lipochromes, which color the eggs or egg shells, occur in species of *Pomacca*, but are absent in the eggs of *Pila* and *Lanistes* (Comfort, 1947). Eggs of *Marisa cornuarietis* are peculiar in possessing an orange pigment when first deposited, but this soon disappears (Michelson, 1956).

The presence of an egg-shell is biologically significant and may be of phylogenetic importance. Both *Pila* and *Pomacca* produce such eggs, and in both cases the eggs are deposited out of water. *Marisa* is completely aquatic and its eggs are gelatinous. Eggs of *Lanistes* were initially reported as membranous by D'Ailly (Pilsbry and Bequaert, 1927), but recent observations have demonstrated that they are gelatinous and are deposited below the water-line (McMahon et al., 1957). Information concerning the eggs of *Asolcne* is limited to a report by von Ihering (*vide* Pilsbry, 1933) in which it is stated that the eggs are gelatinous. The eggs of *Saulea* and *Afropomus* have not been described.

III

The soft parts of 8 species of Pilidae (representing the genera *Pila*, *Lanistes*, *Afropomus*, *Pomacea*, and *Marisa*) were examined for characteristic anatomical differences. Only two structures, the kidney and the penial complex, appeared promising in this respect.

The identity and sources of the material used in this study are presented in Table 1. Specimens of *Pila*, *Lanistes*, *Afropomus*, and the South American *Pomacea* were obtained from the collections of the Museum of Comparative Zoology, Harvard University, through the courtesy of Dr. William J. Clench. These specimens were fixed either in Bouin's solution or 70% ethyl alcohol and subsequently stored in 70% alcohol. Specimens of *Marisa* and *Pomacea paludosa* obtained from laboratory colonies were first relaxed in boiled water and subsequently fixed in Bouin's, Zenker's, or Newcomer's solution. Since not all specimens were fixed in the same way only gross and micro-anatomical features were studied. For micro-anatomical study, tissues were embedded in paraffin, sectioned at 9-12.5 μ , and stained with Lillie-Mayer hemalum and eosin. A total of 82 snails were examined including at least 5 specimens of each species.

A. *The Kidney*. The kidney of members of the Pilidae is composed of two distinct regions, an anterior and a posterior chamber. The anterior chamber is a discrete tubular structure that partially extends into the mantle cavity opening into it through an excretory pore. The posterior chamber is embedded in its entirety in the visceral mass. This chamber is not compact, but consists of a large vacuolated area surrounded laterally and ventrally by a thin, transparent membrane, and bounded dorsally by a large shield-like mass of tissue. The posterior chamber is further limited anteriorly by the pericardial membrane, although access to the pericardium is provided by the renopericardial pore. Descriptions of the kidney of specimens representing the various genera follow:

Pila. In *P. globosa* (Fig. 1E) the dorsal surface of the posterior chamber is broadly rectangular and measures approximately 1.8-2.0 times the length of the anterior chamber. The dorsal surface is brown and blood vessels are not prominent. The anterior chamber is triangular and is so oriented that its main axis is continuous with the axis of the posterior chamber. The kidney in the species from Siam was morphologically similar.

Lanistes. In *L. boltanecanus* (Fig. 1 C) the dorsal surface of the posterior chamber differs from that of *Pila* in being broader anteriorly. The ratio of the length of the posterior chamber to the anterior chamber is approximately 0.8:1 to 1.1. The anterior chamber is considerably longer than in *Pila* and is triangular in shape. The main axis of the anterior chamber in *Lanistes* is also oriented so that it is continuous with the axis of the posterior chamber.

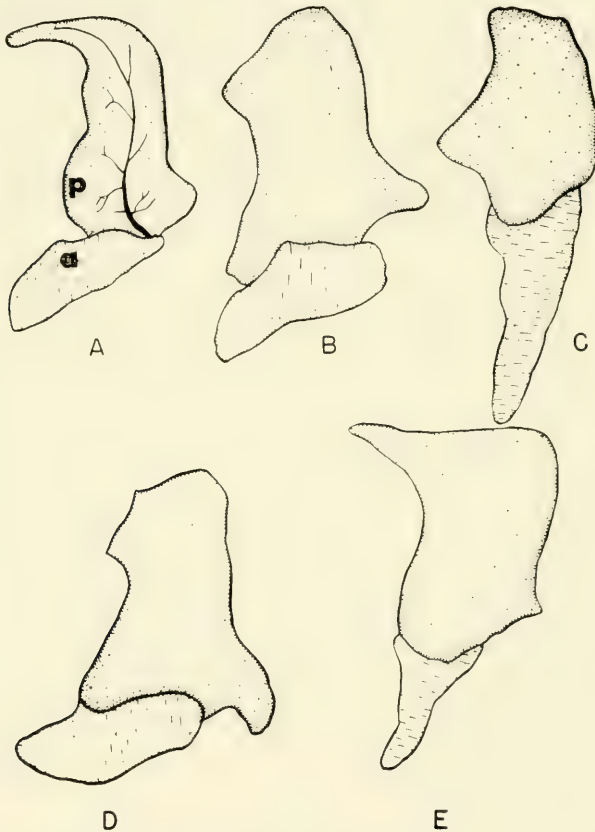


Figure 1. Semi-diagrammatic sketch of the dorsal surface of the kidney in five species of Piliidae: (A) *Afropomus balanoideus*, (B) *Pomacea paludosa*, (C) *Lanistes boltanecanus*, (D) *Marisa cornuarietis*, (E) *Pila globosa*. The posterior chamber (*p*) and the anterior chamber (*a*) of each kidney illustrated are oriented as in Figure 1A.

Afropomus. The kidney in *A. balanoideus* (Fig. 1 A) differs most radically from those of the other genera. The posterior chamber is distinctly triangular in shape and its apex is reflected to the right. Furthermore, it is the only form in which blood vessels are prominent on the dorsal surface of the kidney. The anterior chamber is irregularly rectangular in shape, and its axis lies at an obtuse angle to that of the posterior chamber.

Pomacea. The morphology of the kidney was similar in the four species examined. In *P. paludosa* (Fig. 1 B), the posterior chamber is broadly rectangular and has a prominent protuberance situated anteriorly on its left margin. The anterior chamber is irregular in shape and its long axis lies at an obtuse angle to the axis of the posterior chamber.

Marisa. The kidney of *M. cornuarietis* (Fig. 1 D) is very similar to that found in species of *Pomacea*, thus further strengthening the suggestion that *Marisa* should be considered a subgenus of *Pomacea* (Baker, 1930; Pain, 1950). The lateral protuberance of the posterior chamber in *Marisa* is larger and farther anterior than in *Pomacea*. In addition, the posterior chamber surrounds the anterior chamber more completely in *Marisa* than in *Pomacea*.

B. *The Penial Complex*. The penial complex in the members of the Pilidae arises from the mantle as a finger-like projection. It consists primarily of a large outer penial sheath which enfolds the true penis. Since there is no direct connection between the penis and the vas deferens, sperm must be transmitted from the latter organ to the former, and thence to the female. Sawatkin (1920) first described the presence of an internal sperm canal in the penis of *Ampullaria gigas*. Prashad (1925), however, found that in *Pila globosa* an external sperm canal was present. Our study indicates that both workers were correct and that an internal canal is characteristic of the New World species and an external canal characteristic of the Old World species (Figs. 2-4).

IV

Although additional studies will be needed to establish the generic limits in the family Pilidae, there appears now to be sufficient information to separate the Old from the New World genera, as shown in Table 2.

It is apparent from the foregoing that sufficient data are not available to permit a critical interpretation of the phylogenetic relationships within the family. Nevertheless, there appears to be an evolutionary trend towards the establishment of the family in the terrestrial biotope. The presence of a respiratory sac, in addition to gills, suggests a morphological adaptation for the transition from the aquatic to the terrestrial habitat. Species in two genera (*Pila* and *Pomacea*) are highly amphibious and even deposit their egg masses out of water; the presence of a calcareous egg shell further reduces the dependence of *Pila* and *Pomacea* on an aquatic habitat. If the premise is accepted that the family Pilidae is evolving towards a terrestrial mode of life, then we must conclude that both *Pila* and *Pomacea* represent evolutionary advances in that direction.

TABLE 1
The Specific Identity, Origin, and Number of Specimens Examined

Species	Origin	No. Specimens Examined
<i>Pila globosa</i> Swainson	Calcutta, India,	7
	Bangkok, Thailand	5
<i>Lanistes boltanicanus</i> (Röding)	Cairo, Egypt	10
<i>Afropomus balanoideus</i> (Gould)	Liberia	8
<i>Marisa cornuarietis</i> (Linné)	Río Piedras, Puerto Rico	15
<i>Pomacea paludosa</i> Say	Miami, Florida	12
<i>Pomacea interrupta</i> Sowerby	Chonta antieline, Peru	10
<i>Pomacea columellaris</i> Reeve	Huanuco, Peru	10
<i>Pomacea nublila</i> Reeve	Huanuco, Peru	5

TABLE 2A
Diagnostic Characteristics of the Major Genera of the Family Pilidae¹

Genus	Shape of Shell	Operculum	Respiratory Siphon	Sperm Canal
<i>Pila</i>	Dextral; sub-ovate to globose	Calcareous	Brevisiphonate	External
<i>Lanistes</i>	Sinistral; sub-ovate, turbinate, or carinate	Corneous	Brevisiphonate	External
<i>Afropomus</i>	Dextral; globose	Corneous	Brevisiphonate	External
<i>Saulca</i>	Dextral; sub-ovate	Corneous	?	?
<i>Pomacea</i>	Dextral; sub-ovate, ovate, or globose	Corneous	Longisiphonate	Internal
<i>Marisa</i>	Dextral; secondarily planorboid	Corneous	Longisiphonate	Internal
<i>Asolenc</i>	Dextral; sub-ovate, ovate, or neritoid	Corneous	Longisiphonate	?

¹The morphological characteristics of the kidney of each genus are presented

TABLE 2B

Diagnostic Characteristics of the major Genera of the Family Pilidae¹

Genus	Nature of Eggs	Oviposition Site	Behavior	Geographical Distribution
<i>Pila</i>	Calcareous shell; non-pigmented	In banks or mudflats near water	Highly amphibious	Africa and Asia
<i>Lanistes</i>	Lacking shell; gelatinous; non-pigmented	On submerged vegetation, etc.	Aquatic or slightly amphibious	Africa
<i>Afropomus</i>	?	?	?	Africa
<i>Saulea</i>	?	?	?	Africa
<i>Pomacea</i>	Calcareous shell; pigmented	On emergent parts of aquatic vegetation	Moderately amphibious	South America; Central America; West Indies Southern U.S.
<i>Marisa</i>	Lacking shell; gelatinous and pigmented when first deposited	On submerged vegetation, etc.	Aquatic	South America; West Indies
<i>Asolene</i>	Lacking shell; gelatinous; pigmented (?)	On submerged vegetation, etc.	? Aquatic	South America

¹ The morphological characteristics of the kidney of each genus are presented in Fig. 1.

Figure 2. Cross-section through the penial sheath (*ps*) and penis (*p*) of a specimen of *Pomacca paludosa*. The location of the internal sperm canal is indicated by the arrow. The anatomy of the penis demonstrated in this figure is similar to that observed in all species of *Pomacca* examined. Hemalum and eosin, X47.

Figure 3. Cross-section through the penial sheath and penis of a specimen of *Marisa cornuarietis*. The arrow points to the internal sperm canal. Hemalum and eosin, X29.

Figure 4. Cross-section through the penial sheath and penis of a specimen of *Lanistes boltaneanus*. The arrow points to the external sperm canal. A similar type of sperm canal was found in the penes of specimens of *Pila globosa* and *Afropomus balanoideus*. Hemalum and eosin, X43.



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